

# Morphology and ecology of seedlings, fruits and seeds of Panamá: Vochysiaceae

NANCY C. GARWOOD

Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

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**SYNOPSIS** Seedlings, saplings, fruits and seeds of *Vochysia ferruginea* (Vochysiaceae) are described, and ecological data on these stages summarized, as part of the ongoing *Seedling Flora Project* centred on Barro Colorado Island, Panamá. Seedlings of two other species reported from Panamá are also described. The morphology of these stages is compared to that of other taxa in the family. The potential use of seed and seedling characters in phylogenetic studies within the family is discussed. Special attention is drawn to unusual two-parted cotyledonary stipules, ontogenetic changes in leaf hair morphology, and complex ptyxis and vernation of the embryonic cotyledons.

## INTRODUCTION

The aim of the *Seedling Flora Project*, initiated in 1985, is to produce an illustrated flora of seedlings, saplings, fruits and seeds for the neotropical forest centred on Barro Colorado Island, Panamá (see Garwood & Humphries, 1993; Garwood, 1994, 1995, in prep.). This is the account of *Vochysia ferruginea* Mart. (Vochysiaceae). It is the most abundant *Vochysia* in Panamá, common in the younger forests of Barro Colorado Island and Central Panamá; four other species are known, but only from a few collections (Robyns, 1967a, b; Croat, 1978; D'Arcy, 1987). Ranging from Central America through the Amazon basin, *V. ferruginea* is also the most widespread species in the genus, in contrast to most species which have relatively limited distributions (Stafleu, 1948). Because of its fast growth rate and valuable timber, *V. ferruginea* has been identified as a potentially important forestry species for use in plantations or managed secondary forests in the neotropics (Finegan, 1992; Condit et al., 1993; Butterfield & Fisher, 1994).

In this account, I describe the seedlings, saplings, fruits and seeds of *V. ferruginea*, and the seedlings of two other species known from Panamá, then compare these stages to those of other species in the family to identify characters of potential phylogenetic importance. Fruit and seed characters have been important in delimiting the

tribes and genera of Vochysiaceae; subgeneric classifications and keys to species, however, have been based almost solely on floral and vegetative characters (Warming, 1875; Stafleu, 1948–1954; Keay & Stafleu, 1953). There have been few comparative studies of the gross morphology or anatomy of fruits and seeds (Corner, 1976; Boesewinkel & Venturelli, 1987). Seedlings of few species have been described in detail (del Amo, 1979; Ricardi et al., 1987; Flores, 1993a, b).

## METHODS

Standard methods for germinating seeds, producing voucher specimens for each seed collection, growing and harvesting seedlings, collecting unvouchered seedlings (wildlings) from the forest, and manipulating the descriptive database were developed for the *Seedling Flora Project* (Garwood, 1994, 1995) and were used for this account. The detailed descriptions follow the standard format developed for the *Project*. Descriptive terms have been standardized for use across all families in the *Project*, but generally follow common use. See de Vogel (1980) for definitions of seedling-specific terms and Corner (1976) and Boesewinkel & Bouman (1984) for seed-specific terms. To facilitate identifying isolated seeds, the base of the

seed is arbitrarily defined as the part nearest the hilum, rather than using a reference point within the fruit. Leaf nodes of seedlings are numbered sequentially from the first leaf-bearing node above the cotyledons. The following less conventional terms are used: for length of pubescence or size of other surface features – minute (<0.1 mm), short (0.1–0.5 mm), long (0.5–1.0 mm), very long (> 1.0 mm); for relative thickness of the seed coat or pericarp layers compared to total width of the structure – very thick (> 25% width), thick (10–25%), thin (1–10%), and very thin (< 1%).

## VOCHYSIACEAE

**HABIT AND DISTRIBUTION.** Trees or shrubs, rarely subshrubs. Neotropical except for one very small African genus; 6–8 genera and c. 200 species, 3 genera and 8 species from Panamá, 1 genus and species known from Barro Colorado Island.

**TAXONOMIC REFERENCES.** Stafleu (1948), Keay & Stafleu (1953), Robyns (1967*a, b*), Cronquist (1981), D'Arcy (1987), Kawasaki (in press).

### *Vochysia* Aubl.

**HABIT AND DISTRIBUTION.** Trees, shrubs or rarely subshrubs. Neotropical; c. 100 species, 5 species in Panamá, 1 species known from Barro Colorado Island.

***Vochysia ferruginea* Mart. in Mart. & Zucc., *Nov. Gen. sp. pl.* 1: 151, t. 92 (1824).**

Fig. 1.

**HABIT AND DISTRIBUTION.** Trees, 6–35 m tall, of moist to wet lowland and premontane forests, usually in secondary forest. Nicaragua to Peru and Brazil.

**COLLECTIONS.** Panamá. Barro Colorado Island: *Garwood* 1630A (F, BM, PMA, adult vouchers), *Garwood* 1630B–F (seedlings), *Garwood* 2005 (seedlings), *Foster* s.n. (seedlings with fruit voucher); 50 seedlings to 37 cm tall examined.

### Fruits

*Infructescences* terminal and upper-axillary thyrses, of 1- to 5-flowered helicoid cymose branches, usually with  $\leq 1$  fruit maturing per branch. Rachis densely short-pubescent, with hairs 2-branched,  $\pm$  sessile to short-stalked, appressed to ascending, straight to sinuous; lateral branches (including pedicels) 8–15 mm long, slightly to moderately pubescent. *Receptacles* undeveloped. *Stipes* absent. *Fruits* dry capsules, from superior ovaries. Capsules  $\pm$  woody, loculicidally dehiscent; completely septate; 17–26  $\times$  8–12  $\times$  8–12 mm; straight; oblong to obovate in outline, 3-lobed to 3-cleft in t.s., not compressed; margins entire; base rounded to abruptly truncate; apex rounded to slightly retuse, with stylar scar to 1 mm wide; surface dark brown to black-brown, dull, slightly to prominently warty, often irregularly clear- to white-scaly, glabrous. Seeds 1–3, 1 per

locule, intermediary, separated by mesocarp and endocarp, compressed laterally; long axis of seed radially parallel to long axis of fruit. *Placentae* axile. *Funicle* absent. *Valves* 3, dehiscent from apex, slightly spreading apart then each folding back, remaining firmly attached at base. *Fruit wall* thick, 0.4–1.5 mm wide, thickest centrally, 3-layered. *Exocarp* very thin,  $\approx$  0.05 mm wide,  $\pm$  hard-papery, dark brown to black-brown. *Mesocarp* thick, 0.2–1.3 mm wide, thickest centrally between locules, hard-spongy to  $\pm$  woody, with 2 large longitudinal resin-filled canals near axis between each pair of locules and several smaller chambers along locules (resin drying red-brown and glassy), light to medium brown. *Endocarp* thin,  $\approx$  0.1 mm wide, crustaceous, cream to light brown; inner surface smooth, minutely transversely fibrous, glabrous, glossy, medium brown-orange. When fruit unripe, exocarp grey-green.

### Seeds

Seeds 20–25  $\times$  5–6  $\times$  1–2 mm; hilar-anatropous; 1-winged; transversely half-obovate in outline, compressed and elliptic in t.s. in seminiferous area, planar in wing; margins constricted distally in seminiferous area on hilar side, constricted below wing on opposite side; base widely truncate; apex widely rounded; outer surface  $\pm$  smooth to slightly rough, minutely rough under hairs at higher magnification, densely long- to very long-pubescent, with hairs sinuous, appressed, light to medium brown-orange; glossy, medium brown to brown-orange, dark brown under hairs; not exfoliating. Wing lateral, fibrous,  $\approx$  15–17  $\times$  5–6 mm,  $\pm$  half-elliptic in outline, planar, asymmetrically rounded at apex, entire along margins, with curved ridge slightly raised,  $\pm$  flattened, extending from base to  $\frac{3}{4}$  length of wing and forming thickened straight margin; formed from very long, interwoven, testal hairs. Seminiferous area lateral,  $\approx$  10–11  $\times$  4–5 mm,  $\pm$  elliptic in outline, compressed, darker than wings, with short fringe of interwoven hairs on side opposite wing. *Aril* absent. *Sarcotesta* absent. *Hilum* basal, along straight side, exposed, flush, light brown, lighter than testa, linear, 7–10 mm long. *Micropyle* subbasal to marginal (visible internally at tip of radicle, possibly continuing through thickened ridge of wing and terminating along straight side past hilum), concealed externally. *Lens* absent. *Storage reserves* absent. *Embryo* large,  $\approx$  10–11 mm long, filling seminiferous area, straight,  $\pm$  oblong or ellipsoid, compressed; axis well-developed, with long 4-winged hypocotyl separated from very short radicle by annular ridge at collet, half-exposed; cotyledons well-developed, thin, with compressed obliquely supervolute ptyxis and convolute (*sensu* imbricate) vernation, with wider side of each cotyledon angled down and partially enclosing hypocotyl, with shape obscured by folding and base hidden within folded blade; plumule rudimentary. *Vascular bundle* half-lateral on hilar side, unbranched, thin, with tip exposed at end of hilum and fragments of the funicular bundle often exposed in hilum; passing through short raphe, terminating marginally at tip of seminiferous area. *Seed coat* very thin,  $\pm$  papery, undifferentiated at maturity. *Testa* very thin,  $\pm$  thicker under hilum and around micropyle,  $\pm$  papery, 1-layered, medium to dark brown, densely long-pubescent (see above); inner surface irregular and minutely rough, glabrous, glossy, dark brown. *Tegmen* absent.

**Fig. 1** *Vochysia ferruginea* Mart. Fruit: A, undehiscent fruit; B, dehiscent capsule; C, t.s. Seed: D, seed, lateral view; E, embryo in seminiferous region, with seed coat partially removed; F, embryonic cotyledon and radicle, with one side of cotyledon unfolded and second cotyledon removed to show primary veins, radicle, and angle of folding; G, t.s. through seminiferous region at level marked by arrow in E–F, view toward radicle and wing. Seedling: H, seedling; J, cotyledon; K, cotyledonary stipules, hypocotyl, and petiole ridges; L–M, cotyledonary stipules after epicotyl expands; N, first leaf; O, stipules at first node. Sapling: P, young sapling; Q, branched sapling; R, leaf at node 15; S, stipules at about node 20. Scale bars: black or black and white, 1 mm units; white only, 1 cm units. Symbols: ac, annulate collet; ab, abaxial surface of cotyledon; ad, adaxial surface of cotyledon; c<sub>1</sub>–c<sub>2</sub>, cotyledons 1 and 2; en, endocarp; ex, exocarp; m, midvein of cotyledon; ms, mesocarp; r, radicle; rc, resin canals; sd, seed; so, outline of seed (dotted line); ts, testa; f<sub>1</sub>–f<sub>4</sub>, folds of cotyledon.



*Seedlings and saplings*

Seedlings phanero-epigeal with photosynthetic cotyledons.

**DEVELOPMENT.** Radicle emerges from hilar side of seed near wing. Hypocotyl elongates into loop, then straightens, often carrying seed upward. Cotyledons emerge from seed and fully expand before first leaves are initiated. Shoot rest period is short during the cotyledon stage, about 1 month in sun and 3 months in shade. Seed reserves are exhausted by the end of this period, as albino seedlings die at the cotyledon stage without initiating any leaves. Growth is continuous, with a pair of leaves initiated about every month in sun and every 2–3 months in shade, although shade-produced leaves are smaller.

**ROOTS.** *Primary root* 30–50 × 0.6–0.8 mm, circular in t.s., slightly sinuous, cream to white, becoming medium orange-brown; narrow annular ridge encircles axis at collet, becoming indistinct with age; surface texture and colour between hypocotyl and root change conspicuously and abruptly at collet. *Secondary roots* to 0.2 mm wide, sinuous, very sparsely scattered along primary root. *Root hairs* appear abruptly and densely on primary root just below collet. *Sapling root system:* taproot thick, long-tapering; secondary roots ± thin and common along primary root; tertiary and higher order roots very fine and numerous.

**STEMS.** *Hypocotyl* 15–67 × 0.25–0.50 mm, ± square in t.s., becoming circular in t.s. and hollow with age; 4-ridged to 4-winged, each wing to 0.5 mm tall, continuing at apex into lower margin of cotyledon petiole and terminating at base abruptly above collet; glabrous; medium yellow-green to green, becoming dark brown or red-brown. *Epicotyl* 3–12 × 0.3–0.5 mm, ± square in t.s., becoming circular with age, 4-winged, each 0.3–1.0 mm tall and terminating apically in stipules, glabrous or sparsely short-pubescent, medium green to yellow-green. Hairs short, T-shaped (ratio of arm lengths ≈ 1:1), ± sessile, appressed, straight, and light brown to orange-brown. *Cataphylls* absent. *Internodes* 1–10, 2–15 mm long; later internodes to 34 mm; similar to epicotyl except later internodes becoming densely short- to long-pubescent, with hairs long, unequally 2-branched (arm length ratio to 8:1), short-stalked, ascending, and curved or sinuous or coiled. *Older stems* dark brown, with wings often red-brown, hollow, often sparsely pubescent with age; wood cream-coloured. *Lenticels* appearing on stems > 2 mm wide, sparse on stems 2–4 mm wide; mostly 0.5 mm long, ± round to elliptic, light brown, lighter on dark stems. *Buds:* Cotyledonary buds hidden in axils and inconspicuous above cotyledon scars, rarely protruding to ≈ 0.5 mm in older seedlings, moderately short-pubescent. Lateral buds usually slightly protruding out of axils, to 1 mm long at later nodes, moderately pubescent at early nodes to densely pubescent at later nodes, with accessory bud above sylleptic branches at later nodes. Terminal buds naked, partially covered by stipules, moderately short-pubescent at early nodes to densely long-pubescent at later nodes, with hairs light brown to orange-brown.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent at least until node 3 matures, falling sometime before node 9 matures (between 9 and 20 months). Blades 10–15 × 13–23 mm; straight, flat, depressed obovate, with right half (viewed from the lower abaxial side) usually slightly larger, 2-lobed to 2-cleft; apex of lobes obtuse to broadly obtuse; base emarginate or cordate, often asymmetrical with right lobe slightly larger, or half-rounded/half-cordate; margins entire. Blades glabrous; green above, lighter below. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3; moderate-sized; impressed to slightly raised above, moderately raised below; central primary vein forked, with straight stem  $\frac{1}{2}$ – $\frac{3}{4}$

distance to apex and branches slightly recurved; lateral primary veins basal, ≈  $\frac{3}{4}$  length of blade, straight to curved, diverging at narrowly acute angle, looped, joining branches of central vein to form large ± triangular to obovate intercostal area, the pair of intercostal areas usually spanning about 60–70% of the width of the cotyledons. Secondary veins moderate-sized basally along lateral primaries becoming fine apically; 16–24, 2–4 along midvein, 6–10 along lateral primaries, 6–10 along branches of midvein; mostly marginal, alternate along midvein;  $\frac{1}{6}$ – $\frac{3}{4}$  length of blade (mostly  $\frac{1}{6}$ – $\frac{1}{4}$  along branches of midvein), longest basally; mostly curved or arched along lateral primaries, hooked along branches of midvein, curved to zigzag along midvein, rarely scythe-shaped; diverging at narrowly acute angles (< 45°) basally on lateral primaries to perpendicular angles along branches of midvein; looped marginally, sometimes percurrent in intercostal area, mostly obtusely joined; slightly raised above, slightly raised below. Inter-secondary veins absent. Tertiary veins reticulate within intercostal area, looped in marginal area. *Petioles* 0.5–1.5 mm long, transversely oblong in t.s., straight to slightly curved, 2-ridged above, with ridges continuing into lateral primary veins, 4-winged along margin, with lower wings continuing into hypocotyl wings and upper wings terminating in fleshy knobs near centre of hypocotyl, glabrous. *Stipules* usually fused and interpetiolar, sometimes separate and paired; composed of two structures, both variable in shape and development. The lower part usually a ± conical projection between the petioles at the base of the upper marginal ridge of each petiole, sometimes with two or three separate projections or these absent, mostly 0.125–0.25 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a flattened interpetiolar scale-like outgrowth just above the petioles, initially folded over the terminal bud, becoming erect and visible as the epicotyl expands, 0.25–0.5 mm tall and 0.5–0.75 mm wide, ± transversely oblong to depressed ovate, usually 2- to 5-lobed or -cleft, but sometimes divided into two separate parts or unlobed, the apex of lobes gland-like when young; persistent, papery, green becoming light brown.

**LEAVES.** Opposite, decussate on trunk axis, distichous on branches; simple; short-petiolate, stipulate. Leaf blades 17–32 × 3–9 mm at first node; 20–67 × 5–20 mm at nodes 2–10; to 142 × 49 mm at later nodes; 65–125 × 25–37 mm on branches; straight; narrowly elliptic at nodes 1–3, narrowly elliptic or narrowly obovate at later nodes, elliptic or narrowly elliptic or narrowly obovate or linear-obovate on branches; apex narrowly obtuse or acuminate at nodes 1–10, acuminate to long-acuminate at later nodes and on branches, mucronate at most nodes; base mostly attenuate at early nodes, sometimes narrowly cuneate at later nodes, mostly acute on branches; margins entire, sometimes undulate. Blades green above, lighter below; flat between secondary veins above when fresh; papery; densely minutely pustulate below (from internal crystals), but weakly so at nodes 1–2; densely minutely pustulate above, with pustules usually white on larger leaves; slightly to moderately short- to long-pubescent on blade and veins below at early nodes becoming densely long- to very long-pubescent only on the midvein at later nodes; glabrous on blade above, slightly to moderately ± short-pubescent on midvein at early nodes to densely long-pubescent at later nodes; slightly to moderately short- to long-pubescent along margin, often also densely minute-pubescent when young at later nodes; pubescence light brown to orange-brown. Hairs on midvein above simple, ± erect, straight to slightly curved, mostly 0.5–0.75 mm long on first node, to 1–2 mm long on later nodes; those on blade and veins below T-shaped (ratio of arm lengths ≈ 1:1), ± sessile, appressed and straight at early nodes, mostly 0.25–0.75 mm long, becoming progressively more unequally 2-branched (ratio of arm lengths mostly

< 4:1 on blades but to 8:1 on midvein), short-stalked, ascending, curved or sinuous or coiled at later nodes; those on margins T-shaped or 2-branched (as above) and, at later nodes, also minute, simple, ± erect and sinuous. *Young leaves* conduplicate, spreading open before half-grown, densely pubescent, light green, rigid, erect to horizontal. *Venation* pinnate; brochidodromous. Midvein moderate-sized; straight; flush to slightly raised above, impressed at later nodes and when fresh, prominently raised below. Secondary veins ± fine; 14–17 on leaves at first node, 15–30 at nodes 2–10, to 30 at later nodes and on branches; alternate; mostly  $\frac{1}{6}$ – $\frac{1}{3}$  length of blade, longest centrally; mostly hooked or arched, sometimes also slightly zigzag; diverging at moderately acute angles (45°–65°); looped, sometimes diffusely looped basally on larger leaves, obtusely joined; slightly raised above, slightly raised below. Inter-secondary veins infrequent. Tertiary veins reticulate within intercostal area, looped in marginal area. *Petioles* 0.5–4.0 mm long, ≤ 2 mm long at nodes 1–10; ± circular in t.s., straight to slightly curved; shallowly channelled, with erect narrow margins above; sparsely to moderately pubescent. *Stipules* paired; 0.5–1.0 mm long at nodes 1–6, to 3 mm long at later nodes and on branches; simple, triangular to narrowly triangular; persistent, ± papery; densely pubescent, pale against dark older stems; the inner margin and base continuing to and perhaps above the petiole; the outer margin and base usually terminating abruptly, but sometimes forming a low interpetiolar ridge with the stipule of the opposite leaf as the stem thickens at early but not later nodes.

**ARCHITECTURE.** Trunk axis monopodial to at least 37 cm tall (based on one individual). Initial axis orthotropic. Branches plagiotropic but ± ascending, with leaves distichous through twisting of internodes; sylleptic; alternate and perpendicular at two consecutive nodes (semi-decussate); first produced 31–34 cm above the collet (at about nodes 17–18). First branch internode 60–75 mm long, much longer than superadjacent trunk internode (10–30 mm). First branch leaf half- to full-size of later branch leaves. Single or paired sylleptic secondary branches were produced on the primary branches 24–29 cm from the trunk. Leaves held horizontal. Several factors indicate that growth of the trunk axis above the branches stopped or slowed considerably while the branches were developing, so that overall growth of the trunk was rhythmic (see Fig. 1Q): the trunk axis was very short (about 4 cm long) compared to the length of the branches (28–38 cm long); it was non-woody and very thin compared to the woody internodes on the trunk below the branches and on the lower parts of the branches; and it had matured only one pair of leaves compared to 7–8 pairs on the branches. At the time of harvest, the trunk axis had re-initiated growth, although the primary and secondary branches were still elongating. Rhythmic growth, if substantiated, would suggest Massart's model.

### Ecology

**PHENOLOGY.** In Panamá, *Vochysia ferruginea* usually flowers from late March to early July, and sometimes to a lesser extent in September–October, and its fruits mature August–October (Croat, 1978). Ripe fruits were dehiscent and releasing mature seeds in October (Garwood 1630A). Elsewhere in Central America, it primarily flowers in April–June and October–December and fruits July–September and December–January (Croat, 1978; Flores, 1993b; Moreira & Arnáez, 1994).

**DISPERSAL.** When ripe, valves of the dark brown capsules open and fold back, exposing the glossy bright orange-brown endocarp and releasing the seeds. Seeds are wind-dispersed.

**VIABILITY.** Seeds remain viable for 2–3 months when stored at ambient temperature (24–26°C) and moisture levels if well-aerated

(Flores, 1993b). Flores (1993b) considers the seeds orthodox, although the initial moisture content of the seeds (23%) is rather high.

**GERMINATION.** Seeds germinate rapidly (13 days) at moderate percentages (39–50%) in both sun and shade in the growing house (this study). Other studies also report rapid germination (8–14 days) in the forest or growing house, but higher germination percentages (80–95%) (Flores, 1993b; Moreira & Arnáez, 1994).

**ESTABLISHMENT AND GROWTH.** The earliest stages of natural seedling establishment and growth have not been studied, although Flores (1993b) noted that germinating seeds and young seedlings suffered high predation from ants and other herbivores. Boucher et al. (1994) reported exceptional seedling densities and sapling growth after Hurricane Joan in Nicaragua in October 1989, which killed all adults in the population. Four months after the hurricane, there were 94 500 seedlings and saplings (0.1–1.5 m tall) per hectare, but few young trees (3.2–10 cm DBH). The extremely open canopy, created by the hurricane through defoliating and felling trees, favoured survivorship and growth of these juveniles, such that young trees were abundant four years later and were growing on average at about 1.4 cm DBH/year. Under the less open canopy of Barro Colorado Island, not recently if ever disturbed by hurricanes, similar-sized individuals (1–9.9 cm DBH) grew on average only 0.45 cm DBH/year, but larger individuals (> 10 cm DBH) grew more rapidly, 1.3–1.7 cm DBH/year (Condit et al., 1993).

The population dynamics and appropriate management strategies for this species may differ greatly in hurricane-prone areas such as Nicaragua compared to hurricane-free areas such as Panamá. Where hurricanes are common in the Caribbean, they occur mostly August–October during the period *Vochysia ferruginea* is maturing and dispersing its seeds. A hurricane occurring late in the season might blow the wind-dispersed seeds over large areas of disturbed forest, expanding the population. An earlier hurricane might kill adult trees before seeds could be matured and dispersed, preventing regeneration from seed and eliminating the local population, unless most regeneration comes from established shade-tolerant juveniles. It is not yet known whether seedling recruitment after disturbance is primarily from recently germinated seedlings from the current year's seed crop or older shade-tolerant juveniles surviving from previous years.

**Vochysia guatemalensis** Donn. Sm. in *Bot. Gaz.* **12**: 131, pl. 22 (1887).

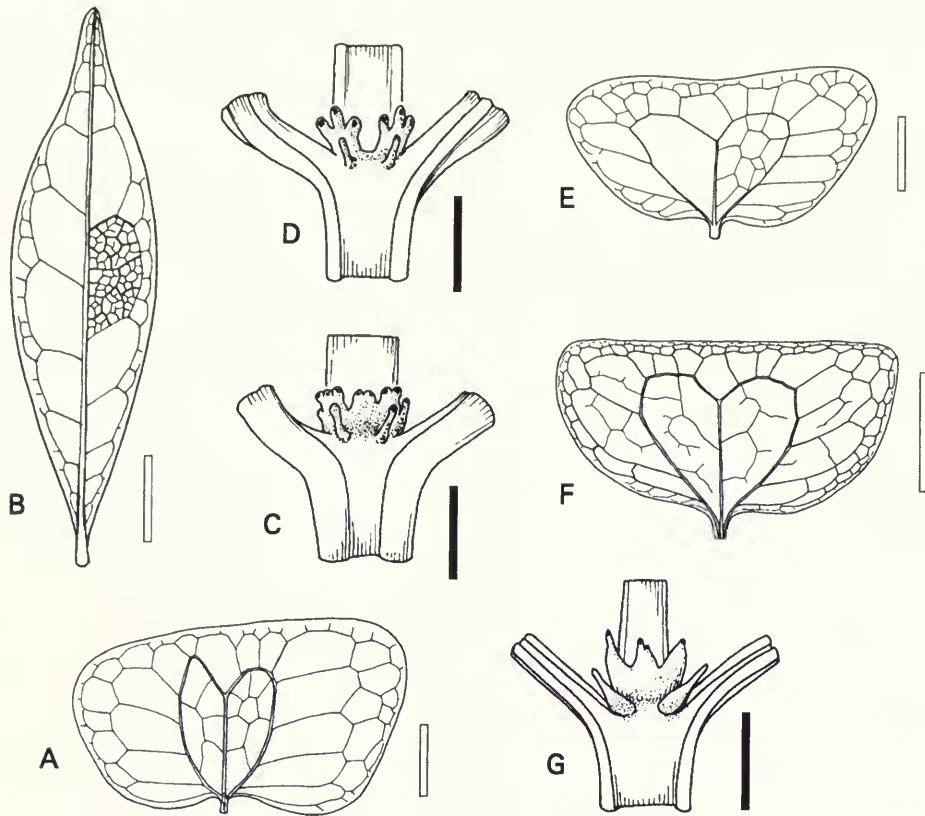
*Vochysia hondurensis* Sprague in *Bull. Misc. Inform., Kew* **1922**: 183 (1922).

Fig. 2A–D.

**HABIT AND DISTRIBUTION.** Trees, 30–55 m tall. Veracruz, México, to Panamá.

**COLLECTIONS.** **Belize.** Cayo District, Chiquibul: Palmar, Garwood 4031 (BM, seedlings with seed voucher); New Maria, *Monro* 867 to 871, *Monro, Howe & King* M4162X, M7231X, M7340X (seedlings) and M6002X (sapling); 28 seedlings to 17 cm tall examined, sapling height about 2 m.

**TAXONOMIC NOTE.** The seeds associated with Garwood 4031 unmistakably identify the seedlings to genus. If one accepts the synonymy of *Vochysia guatemalensis* and *V. hondurensis* (Standley & Steyermark, 1949; Gaos, 1978; Flores, 1993a), then only one species has been reported from Belize (Stafleu, 1948; Standley & Steyermark, 1949). That the mature leaves and stems are nearly glabrous supports the identification of these collections as *V. guatemalensis*.



**Fig. 2** *Vochysia guatemalensis* Donn. Sm. Seedling: A, cotyledon; B, first leaf; C–D, cotyledonary stipules. *Vochysia* sp. Seedling: E–F, cotyledons; G, cotyledonary stipules; E, Hampshire & Whitefoord 269; F–G, Garwood 135. Scale bars: black, 1 mm; white, 1 cm.

#### Seedlings and saplings

Seedlings phanero-epigeal with photosynthetic cotyledons.

**ROOTS.** *Primary root* 30–70 × 0.8–1.2 mm, circular in t.s., slightly sinuous, cream-coloured; narrow annular ridge encircles axis at collet, becoming indistinct with age. *Secondary roots* sinuous, scattered along primary root.

**STEMS.** *Hypocotyl* 50–85 × 1 mm, square to rectangular in t.s., becoming circular with age; 4-ridged or 4-winged, each wing < 0.25 mm tall, continuing at apex into lower margin of cotyledon petiole; glabrous; green. *Epicotyl* 5–22 × 1 mm, ± square in t.s. when young, becoming circular with age; 4-winged, each wing ≤ 0.25 mm tall and terminating apically in a stipule; glabrous; green. *Cataphylls* absent. *Internodes* 1–16, 3–5 mm long; 4-winged, each wing about 0.25 mm tall and terminating apically in a stipule; glabrous; green. Older stems light brown to grey-brown, hollow. *Buds*: Cotyledonary buds hidden in axils, sparsely pubescent. Lateral buds protruding out of axils, ≤ 0.5 mm long at nodes 1–15, sparsely short-pubescent at first node, becoming densely pubescent at later nodes. Terminal buds naked, sparsely pubescent at first node, becoming moderately pubescent at later nodes. Hairs on all buds clear to white, mostly ≤ 0.25 mm long.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent until at least leaves at nodes 2–3 mature. Blades 15–26 × 25–37 mm; straight, flat, ± depressed obovate, with right half (seen from lower or abaxial side) usually larger at both base and apex; apex truncate to emarginate, often obliquely so, rarely ± rounded; base cordate, rounded, to ±

truncate, often obliquely so; margins entire. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3, ± fine, slightly raised above, moderately raised below; central primary vein forked, with straight stem  $\frac{1}{2}$  to  $\frac{3}{4}$  distance to apex and branches slightly curved; lateral primary veins basal, about  $\frac{3}{4}$  length of blade, mostly curved, diverging at narrowly acute angle, looped, joining branches of central vein and forming ± small obovate or triangular intercostal area or rarely branching before joining the central vein and forming a ± indistinct intercostal area, the pair of intercostal areas, when distinct, usually spanning about 30–50% of the width of the cotyledon. Secondary veins moderate-sized basally along lateral primaries becoming fine apically; 12–16, 0–1 along midvein, 8–10 along lateral primaries, 4–5 along branches of midvein; mostly marginal; to  $\frac{2}{3}$  length of blade, longest basally; mostly arched or hooked; diverging at narrowly acute angles basally on lateral primaries to perpendicular angles along branches of midvein; looped marginally, acutely to obtusely joined; flush above, moderately raised below. *Petioles* 2–3 mm long, transversely oblong in t.s., 2-ridged above, with ridges continuing into lateral primary veins; 4-ridged along margins, the lower ridges continuing down into the ridges or wings on the hypocotyl and the upper ridges terminating at the stipules; glabrous. *Stipules* separate and paired or sometimes fused and interpetiolar, composed of two structures, both variable in shape and development. The lower part a pair of ± conical projections between the petioles near the base of the upper marginal ridge of each petiole, one or both sometimes absent, mostly 0.25–0.75 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a pair of flattened scale-like outgrowths between and just above the petioles, initially folded over

the terminal bud but becoming erect and visible as the epicotyl expands, each  $\pm$  ovate to rhombic, 0.5–0.75 mm tall and wide, the apex often 3-lobed and gland-like, the pair sometimes fused together, then 0.5–0.75  $\times$  0.75–1.5 mm tall and wide and the apex multilobed or irregular.

**LEAVES.** Opposite, decussate on seedling trunk axis, sometimes 3-whorled on sapling trunk axis; simple, short-petiolate; stipulate. Leaf blades 30–69  $\times$  11–19 mm at first node; 30–82  $\times$  13–17 mm at nodes 2–15, to 195  $\times$  52 mm on saplings; straight; narrowly obovate to narrowly elliptic at nodes 1–15 and on sapling; apex acuminate or long-acuminate, rarely acute at first node; bases cuneate to narrowly acute; margins entire. Blades green, papery at early nodes becoming subcoriaceous on larger saplings; sometimes moderately pustulate above and below on later leaves, the pustules pale above; the blade nearly glabrous when fully expanded, the midvein below often sparsely short-pubescent, but moderately to densely pubescent on the blade and midvein below and along margins when expanding leaves of seedlings are < 10 mm long. Hairs simple, basifixed, < 0.25 mm long, clear to white. *Venation* pinnate, brochidodromous. Midvein moderate-sized; straight; flush to slightly raised above, prominently raised below. Secondary veins thin, 14–22 at first node, to 22 at later nodes; alternate; mostly  $\frac{1}{4}$  to  $\frac{1}{3}$  length of blade, longest centrally; mostly hooked or arched, diverging at a moderately acute angle; looped, obtusely joined; slightly raised above and below. Intersecondary veins infrequent. Tertiary veins reticulate in intercostal area, looped in marginal area. *Petioles* 1 mm long at first node, to 2 mm long at nodes 2–15, to 7 mm on saplings; shallowly channelled, with erect narrow margins above. *Stipules* paired; 1.0–1.2 mm long at first node, to 1.7 mm long at nodes 2–15; simple, narrowly triangular; the inner margin and base continuing above the petiole and apparently terminating near the lateral bud; the outer margin and base usually terminating abruptly, but sometimes forming a low interpetiolar ridge with the stipule of the opposite leaf as the stem thickens at some early nodes; persistent; often sparsely short-pubescent toward the apex.

### **Vochysia** sp.

Fig. 2E–G.

**COLLECTIONS.** Panamá. Colón Province: Santa Rita Ridge, *Garwood* 135 (seedlings with seed fragment); Chiriquí Province: Fortuna, *Hampshire & Whitefoord* 269 (BM, seedlings); 15 seedlings to 9 cm tall examined.

**TAXONOMIC NOTE.** Specific identification is not yet possible, as *Garwood* 135 had only a seed fragment attached and *Hampshire & Whitefoord* 269 lacked seeds altogether. In addition to *Vochysia ferruginea*, *V. allenii* Standl. & L.O. Williams, *V. jefensis* A. Robyns, and *V. speciosa* Warm. have been reported from eastern Panamá and *V. hondurensis* (= *V. guatemalensis*) from western Panamá (D'Arcy, 1987). As immature leaves of both collections have T-shaped hairs  $\geq$  0.25 mm long on the lower surfaces (see below), it is not *V. guatemalensis*, which has simple basifixed hairs < 0.25 mm long (see above). The T-shaped hairs on the first leaves ally it with *V. ferruginea*, but the cotyledons are about 1.5–2 times larger. Thus, the Chiriquí collection is a new species record for western Panamá. As the cotyledons from the Chiriquí collection are consistently larger than those from the Colón collection (Fig. 3), two species might be represented. Given their similarity and the paucity of material, they are described together below, with the few differences noted.

### *Seedlings*

Seedlings phanero-epigeal with photosynthetic cotyledons.

**ROOTS.** *Primary root* 45–70 mm long, 1 mm wide, circular in t.s., slightly sinuous, medium brown.

**STEMS.** *Hypocotyl* 50–86  $\times$   $\approx$  1 mm long and wide,  $\pm$  square to rectangular in t.s., 4-ridged to 4-winged, each wing  $\leq$  0.25 mm tall and continuing at apex into lower margin of petiole; glabrous. *Epicotyl* (immature) 4-ridged or 4-winged, each wing  $\leq$  0.25 mm tall; glabrous. *Buds:* Cotyledonary buds hidden in axils (*Garwood* 135) or 0.75 mm tall and densely pubescent (*Hampshire & Whitefoord* 269).

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent. Blades 14–21  $\times$  22–40 mm (14–17  $\times$  25–32 mm in *Garwood* 135, 19–21  $\times$  34–40 mm in *Hampshire & Whitefoord* 269); straight, flat, depressed obovate, with right side (viewed from lower or abaxial surface) usually larger than or sometimes equal to left side; apex truncate, emarginate, or cordate, sometimes obliquely so; base rounded, truncate or emarginate, sometimes unequal; margins entire. Blades green, glabrous. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3, moderate-sized; central primary vein forked, with straight stem  $\frac{2}{3}$  to  $\frac{3}{4}$  distance to apex and branches recurved; lateral primary veins basal, about  $\frac{3}{4}$  length of blade, mostly curved, diverging at narrowly acute angle, looped, joining branches of central vein to form  $\pm$  small obovate or triangular intercostal area, the pair of intercostal areas usually spanning about 40–50% of the width of the cotyledon. Secondary veins moderate-sized basally becoming fine apically; 10–16, 0–2 along midvein, 6–9 along lateral primaries, 3–5 along branches of midvein; mostly marginal;  $\frac{1}{3}$  to nearly full length of blade, longest basally; mostly arched to hooked, diverging at narrowly acute angles basally to perpendicularly apically; looped marginally, acutely to perpendicularly joined; flush above, moderately raised below. Tertiary veins reticulate within intercostal areas, looped in marginal areas. *Petioles* about 2 mm long, transversely oblong in t.s., 2-ridged above, with ridges continuing into the lateral primary veins; 4-ridged along margin, with lower ridges continuing into hypocotyl ridges and upper ridges terminating in the stipules; glabrous. *Stipules* usually fused and interpetiolar, sometimes separate and paired; composed of two structures, both variable in shape and development. The lower part a pair of  $\pm$  conical projections between the petioles near the base of the upper marginal ridge of each petiole, sometimes absent or bifid, mostly 0.25–0.5 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a flattened scale-like outgrowth between and just above the petioles, initially folded over the terminal bud but becoming erect and visible as the epicotyl expands,  $\pm$  transversely oblong to depressed ovate, 0.5–0.75  $\times$  0.75–1.0 mm tall, 3- to 5-lobed and gland-like at the apex, sometimes divided.

**LEAVES** (only immature leaves at first node present). Opposite, decussate on trunk axis; simple, short-petiolate. Blades moderately pubescent below and along margins when expanding blades are < 5 mm long, sparsely pubescent when half-expanded. Hairs 0.25–0.625 mm long, T-shaped, sessile, pale orange-brown. *Venation* pinnate, brochidodromous.

### **Key to known seedlings of *Vochysia* in Panamá and Central America**

1. T-shaped hairs present on lower surface of young leaves at first and early nodes
2. Cotyledons 13–23 mm wide and 10–15 mm long ..... ***V. ferruginea***

2. Cotyledons 22–40 mm wide and 14–21 mm long ..... *V. sp.*
1. Simple basifixed hairs present on lower surface of young leaves at first and early nodes or hairs absent; cotyledons 25–37 mm wide and 15–26 mm long ..... *V. guatemalensis*

## DISCUSSION

Vochysiaceae is a moderate-size, primarily neotropical family divided into two tribes. Vochysieae includes *Vochysia* (100 species), *Callisthene* (12 species), *Salvertia* (1 species), and *Qualea* sensu lato (77 species, including *Ruizterania*); Erismeeae includes *Erisma* (16 species) and *Erismadelphus* (2 species), the only African taxa (Stafleu, 1948–1954; Keay & Stafleu, 1953; Marcano-Berti, 1969; Kawasaki, in press). The monotypic *Euphronia* (= *Lightia*), sometimes included in Vochysiaceae (Lleras, 1976; Cronquist, 1981) or segregated as the Euphroniaceae (Marcano-Berti, 1989, 1990), is not closely related to Vochysiaceae according to recent molecular studies (Litt et al., 1995) and will not be further discussed.

## Fruit

There are two basic types of fruit in Vochysiaceae (Warming, 1875; Stafleu, 1948–1954; Keay & Stafleu, 1953). The dehiscent trilocular capsules of Vochysieae, derived from superior ovaries, contain winged seeds. The indehiscent unilocular fruits of Erismeeae, derived from inferior to semi-inferior ovaries, have persistent enlarged winged calyx lobes. Within Vochysieae, fruits of *Callisthene* have a thick persistent central column and a fragile exfoliating exocarp not found in the other genera. Several of the 12 ovules per locule mature into seeds in *Qualea* (Stafleu, 1953); one or more of the few ovules per locule mature in *Callisthene*, (Stafleu, 1952). In *Vochysia* and *Salvertia*, however, only one of the two ovules in each locule usually develops into a mature seed (Warming, 1875; Stafleu 1948; Standley & Steyermark, 1949; Robyns, 1967a; Gaos, 1978; Moreira & Arnáez, 1994; this study), although two mature according to Flores (1993a, b).

Fruits of *Vochysia ferruginea* are typical of the genus (Stafleu, 1948), being 3-locular loculicidal capsules, oblong or obovate in outline and 3-angled. Variation in size, shape, and surface texture of fruits in *Vochysia* is not well-documented: fruits of many species are still unknown (Warming, 1875; Stafleu, 1948; but see van Roosmalen, 1985). The gross morphology of fruits has been little studied. Stafleu (1948) described the pericarp of the genus as consisting of a black or dark bluish exocarp 'strongly adhering to the shining golden-yellow endocarp', an observation repeated by later authors (Robyns, 1967a; van Roosmalen, 1985), but Flores (1993a, b) noted the presence of a well-developed mesocarp in both *V. ferruginea* and *V. guatemalensis*. In *V. ferruginea*, there is a brown to black exocarp, a light to medium brown spongy to woody mesocarp, thickest near the centre of the fruit, and a pale crustaceous endocarp of even thickness around each locule (Fig. 1C). The mesocarp is penetrated by longitudinal resin canals adjacent to the locules (Fig. 1C) and is also well-vascularized (Flores 1993a, b). In mature fruit, the endocarp is as well-developed around empty locules as around those filled with mature seeds, indicating that development of each locule is not dependent on the growth of fertilized ovules within it. The locules complete development before the seeds and determine the shape of the seed wing (Boesewinkel & Venturelli, 1987).

## Seed

Seeds are winged in the Vochysieae. The wings are large and unilateral in *Vochysia*, *Qualea*, and *Salvertia*, but small and circum-

ferential in *Callisthene*, and are formed from compacted testal hairs in *Vochysia* and *Salvertia*, but from extensions of the testa in *Qualea* and *Callisthene* (Warming, 1875; Stafleu, 1948–1953; Boesewinkel & Venturelli, 1987). The seeds of *V. ferruginea* are typical of the genus (Warming, 1875). The wing is on the anti-hilar side of the seed, and the micropyle extends along the seminiferous area and terminates near the hilum, as in *V. pygmaea* Bong. and *Salvertia* (Boesewinkel & Venturelli, 1987). In contrast, the wing of *Qualea* is on the hilar side of the seed, such that the micropyle extends along the anti-hilar margin of the wing and opens at the apex of the wing away from the hilum (Boesewinkel & Venturelli, 1987). The final shape of the wing in *Vochysia* is determined by the shape of the locule: the unicellular hairs grow upward from the testa to fill and take their shape from the empty locule (Boesewinkel & Venturelli, 1987). Hence, much of the variation in size and shape of seeds among species in *Vochysia* probably arises from differences in the size and shape of the mature locules.

There has been little work on seed anatomy of Vochysiaceae (Corner, 1976; Boesewinkel & Venturelli, 1987). Stafleu (1948, 1953) described the testa of *Vochysia* as brown, thin, and chartaceous, and the tegmen as very thin, paper white, and adhering to the testa, and the testa of *Qualea* as chartaceous. The mature seed coat of *V. pygmaea*, however, consists only of the outer layers of the testa, because the inner layers of the testa are crushed and the tegmen resorbed during development (Boesewinkel & Venturelli, 1987). The seed coat also appeared as one undifferentiated layer at maturity in *V. ferruginea* (this study), but Flores (1993a, b) described a dark exotesta distinct from the dead cell layers and air spaces of the mesotesta and endotesta and remnants of the tegmen in *V. ferruginea* and *V. guatemalensis*. In contrast, the mature seed coat of *Qualea densiflora* Warm. and *Callisthene* retains both the inner layers of the testa and tegmen (Boesewinkel & Venturelli, 1987). The seed coat of *Erisma* and *Erismadelphus* is thick and contains a large branched vascular bundle (Boesewinkel & Venturelli, 1987). The vascular bundle of *V. ferruginea*, hitherto undescribed in Vochysieae, is unbranched and terminates at the tip of the seminiferous area. The hilum of *V. ferruginea* (7–10 mm long) is longer than in *V. pygmaea* (3–4 mm long), and stretches over a greater proportion of the length of the winged seed (35–40% versus about 20%). Due to the long hilum, the seed type of *V. ferruginea* is described as hilar-anatropous.

Endosperm is absent in mature seeds of Vochysiaceae (Bentham & Hooker, 1867; Baillon, 1874; Warming, 1875; Petersen, 1896; Stafleu, 1948–1953; Standley & Steyermark, 1949; Robyns, 1967a; Gaos, 1978; Boesewinkel & Venturelli, 1987; Flores, 1993a, b). None was seen in *Vochysia ferruginea*. Occasional reports that endosperm is rarely well-developed (Cronquist, 1981; Niembro Rocas, 1989) do not appear well-founded. A thin, whitish aril, adhering to the testa, was reported in *V. guatemalensis* (Gaos, 1978) and in the family (Niembro Rocas, 1989): this appears to be a mistranslation of Stafleu's (1948) description of the tegmen (see above).

## Embryo

In all genera, the embryo of the mature seed is straight and the plumule and radicle poorly developed (Warming, 1875; Stafleu, 1948–1954). In *Vochysia ferruginea*, the embryonic axis is well-developed; the hypocotyl is relatively long compared to the poorly developed radicle, compressed, 4-winged, and annulate at the collet. The winged hypocotyl and annulate collet persist into the seedling stage, confirming the identification of the structures in the seed. In Vochysieae, the embryonic cotyledons are generally thin, foliaceous, and folded in various ways (see below), whereas, in Erismeeae,



they are thick, fleshy, and not or scarcely folded (Baillon, 1874; Warming, 1875; Boesewinkel & Venturelli, 1987; Kawasaki, in press). The cotyledons of *Erismadelphus* are plano-convex and slightly convolute at the margins (Boesewinkel & Venturelli, 1987), while those of *Erisma* are narrowly elongate and semi-cylindrical (Baillon, 1874), plano-convex (Boesewinkel & Venturelli, 1987), or flat (Stafleu, 1954).

The embryonic cotyledons have been described as unequal in *Vochysia* (Warming, 1875; Stafleu, 1948) and *Salvertia* (Stafleu, 1948), although no comparable information was given for *Qualea* or *Callisthene*. Unequal could mean either that each cotyledon is asymmetrical or that the two cotyledons are heterocotylar, differing in shape or size. Cotyledons are asymmetric in two species of *Vochysia* and one species of *Qualea* but symmetric in one species of *Vochysia* and *Salvertia* (Table 1), based on the illustrations of the unfolded embryo in Warming (1875). In *V. ferruginea*, each cotyledon is usually asymmetric, with the right side (viewed from the lower abaxial surface) larger, at least basally. The base of the smaller side tends to be rounded, and that of the larger side cordate, as in the expanded cotyledon of the seedling (Fig. 1J). The embryonic cotyledons of *V. ferruginea*, when unfolded, and the fully expanded cotyledons of the seedling (Fig. 1H, P), are isocotylar. The larger side of one cotyledon opposes the smaller side of the other on the embryo and seedling, hence, the two cotyledons are identical in shape, not mirror-images.

Most monographic and floristic works indicate that the embryonic cotyledons of Vochysiaceae are folded, but give insufficient detail to characterize the complex pattern of folding. It is usually unclear which component of folding is described: ptyxis, the folding of an individual organ such as a leaf in the bud or cotyledon in the seed, or vernation, the relationship of the immature organs to each other (Bell, 1991). Some terms, such as convolute, are used for both ptyxis and vernation but have different meanings (Bell, 1991). Definitions of terms vary considerably among authors.

In *Vochysia ferruginea*, each cotyledon is folded four times around the longitudinal axis of the embryo (Fig. 1E-G). The folds ( $f_1$ - $f_4$ ) are parallel to the radicle but not parallel to the midvein of the cotyledon (Fig. 1F). The margin of the larger side of the cotyledon (the right side as viewed from the lower abaxial surface) is on the exterior of the embryo, while the margin of the smaller side is in the interior. The folded smaller side is completely enclosed within the folded larger side. The inner margin is narrowly bent back with the adaxial surfaces appressed at the first fold ( $f_1$ ). Because of the oblique folding of the cotyledon, the base of the larger side of each asymmetric cotyledon is folded around the hypocotyl, nearly obscuring it (Fig. 1F). Except for the compressed nature of the embryo and distinct lines of folding, ptyxis is essentially supervolute (often called convolute) but oblique. It is not conduplicate, although the cotyledon appears to be folded around the midvein in cross-sections through the middle of the embryo (Fig. 1G). Vernation is essentially convolute *sensu* Bell (1991), although unusually compressed. Each cotyledon partially overlaps the other, with inner margins opposite near the centre of the embryo and outer margins opposite on the exterior (Fig. 1G). Confusingly, vernation is not convolute *sensu* Radford et al. (1974), because one rolled or supervolute cotyledon is not completely enclosed within a second rolled cotyledon.

Convolute vernation and supervolute ptyxis are also found in *Vochysia pygmaea*, *V. tucanorum* Mart., and *Salvertia convallari-dorea* A. St.-Hil., as seen in transverse sections of the embryo (Warming, 1875: figs 16-II, 17-II; Boesewinkel & Venturelli, 1987: fig. 10B). The embryos are less compressed and angular than in *V. ferruginea*, and the inner margins of the cotyledons overlap rather

than being folded back individually. Embryos of *V. guatemalensis*, *V. obscura* Warm., *V. tucanorum*, and *S. convallari-dorea* (Warming, 1875: figs 13, 16II, 17II; Flores, 1993a: fig. 9) are externally similar to that of *V. ferruginea*, and the position of the outer cotyledon margin is also consistent with convolute vernation. Ptyxis is probably oblique in most species because the hypocotyl is hidden, as in *V. ferruginea*, but may differ in *V. obscura*, given that the hypocotyl is well-exposed in spite of the deeply lobed cotyledon base. Although folding appears somewhat angular in section because the seed is compressed, cotyledons are not plicate in the sense of fan-like. Thus, there is one basic pattern of vernation and ptyxis for cotyledons of *Vochysia* and *Salvertia*, with minor variations, whether cotyledons are asymmetric or not.

Embryonic cotyledons of the genus *Vochysia* have previously been described as convolute or rolled (Bentham & Hooker, 1867; Petersen, 1896; Flores, 1993a, b), spirally convolute (Baillon, 1874), obliquely spirally convolute (Warming, 1875), spirally folded (Boesewinkel & Venturelli, 1987), and spirolobal (Stafleu, 1948). The cotyledons of the species discussed above are not spirolobal, a term now used for bent embryos with incumbent once-folded cotyledons (Duke, 1969; Radford et al., 1974). The remaining descriptions are not inconsistent with convolute vernation and/or obliquely supervolute (= convolute) ptyxis, but do not completely characterize ptyxis and vernation.

In *Qualea*, embryonic cotyledons have been described as convolute or rolled (Petersen, 1896; Boesewinkel & Venturelli, 1987) or convolute and plicate (Warming, 1875; Stafleu, 1953). The cotyledons of *Q. grandiflora* Mart. (Warming, 1875: fig. 8-II) are more complexly folded than in *Vochysia*, although the complete pattern cannot be resolved from the embryo and its cross-section. Supervolute ptyxis and convolute vernation, as in *Vochysia*, can be eliminated, however, and folding may be irregular but is not fan-like. The exposed margins of the cotyledon are very uneven, almost lobed. In contrast, the exposed cotyledon margins of *Q. multiflora* Mart. (Warming, 1875: fig. 7-II) are unlobed and parallel, similar to *Vochysia* except that they are close together on the exterior of the embryo. There appears to have been some folding around the longitudinal axis through the radicle, but the specific pattern is again unknown. In both species of *Qualea*, the folded cotyledons nearly obscure the embryonic axis. Thus, ptyxis and vernation appear very different in these two *Qualea* species compared to the homogeneous pattern observed in *Vochysia*.

Embryonic cotyledons in *Callisthene* have been described as plicate and/or convolute (Warming, 1875; Petersen, 1896; Stafleu, 1952; Boesewinkel & Venturelli, 1987). In *C. major* Mart. (Warming, 1875: fig. 3-II), the embryo is straight and compressed. Each cotyledon is irregularly folded, appearing more wrinkled (corrugate) than plicate on the surface; each margin is involute, folding back with the adaxial surfaces touching. The folded cotyledons are pushed together for most of their length and width, but the folds are only rarely synchronous between the two. The involute margin of the first cotyledon is exposed at the edge of the embryo and overlaps the involute but hidden margin of the second, whereas the exposed involute margin of the second cotyledon abuts, rather than overlaps, the hidden margin of the first. No standard terms describe this pattern of folding, but corrugate-involute ptyxis and semi-convolute or valvate-convolute vernation might be used. In contrast to other genera in Vochysiaceae, the embryonic axis is fully exposed and the embryo appears almost spatulate, except for the wrinkled slightly overlapping cotyledons.

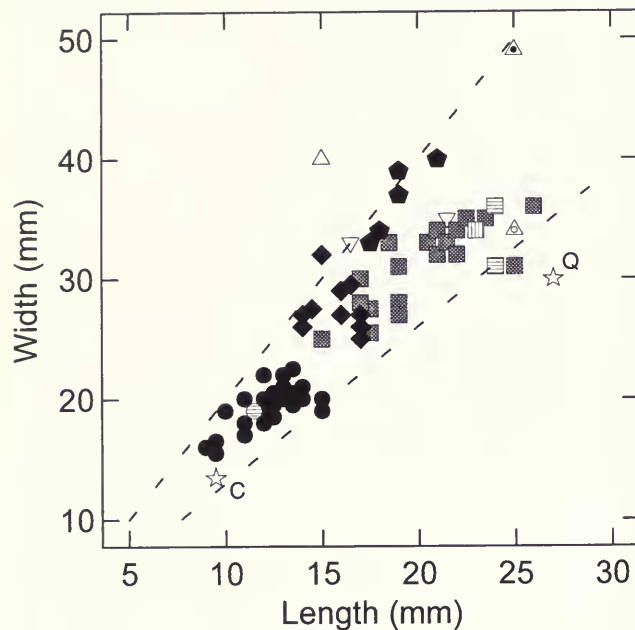
Embryos of *Vochysia*, *Qualea*, and *Callisthene* are rich in lipids and poor in starch, those of *Erisma* are poor in lipids and starch, and those of *Erismadelphus* are rich in lipids and starch (Boesewinkel &

Venturelli, 1987). The seeds of *V. hondurensis* are rich in protein, as well as lipids (Blanche et al., 1991).

## Seedling

There is little published information on seedlings and saplings of Vochysiaceae. Only *Vochysia duquei* Pilg., *V. guatemalensis*, and *V. ferruginea* (del Amo, 1979; Ricardi et al., 1987; Flores, 1993a, b; this study) have been described in detail. Limited data are available for ten additional species and some information can be inferred from the embryos of five species (Tables 1–2). In Erismeeae, cotyledons of *Erismadelphus* are cryptocotylar, hypogeal, and food-storing. Embryonic cotyledons of *Erisma* are also fleshy and food-storing, but it is not known whether these are cryptocotylar or phanerocotylar, or epigeal or hypogeal, after germination. No other information on seedlings is available for Erismeeae.

In Vochysieae, cotyledons are all phanerocotylar, epigeal, and foliaceous (Table 1). Where known, they persist after the first leaves are produced, and presumably continue to photosynthesize. In *Vochysia thyrsoidea* Pohl, they are the major photosynthetic organ



**Fig. 3** Relationship of cotyledon length and width in Vochysiaceae. *Vochysia* species: circles, *V. ferruginea* (Panamá: Garwood 1630; Garwood 2005; Foster s.n.; Costa Rica: Flores, 1993b); squares, *V. guatemalensis* (Belize: Garwood 4031; Monro 868–871, Monro et al. M4162X; del Amo, 1979; Costa Rica: Flores, 1993a); diamonds, *V. sp.* (Panamá: Hampshire & Whiteford 269); octagons, *V. sp.* (Panamá: Garwood 135); inverted triangles, *V. duquei* (Venezuela: Ricardi et al., 1987); open triangle, *V. surinamensis* (Guyana: Polak, 1992); triangle with black circle, *V. sp.* (French Guiana: Oldeman & Fundter, 1986); triangle with white circle, *V. thyrsoidea* (Brazil: Rizzini, 1965). Other genera (stars): *C. Callisthene major* (Brazil: Labouriau et al., 1964); *Q. Qualea grandiflora* (Brazil: Thomazini et al., 1973). Shading of symbols indicates country of origin: black, Panamá; cross-hatching, Belize; horizontal hatching, Costa Rica; vertical hatching, México; white, South America. Dashed lines represent width to length ratios of 2.0 (upper line) and 1.3 (lower line). Data are measurements of all seedlings in each collection, values cited in references, or my estimates from illustrations in references where values are not given. Overlapping points have been off-set by 0.5–1.0 mm to improve readability.

for many months (Rizzini, 1965). Cotyledons range from about 1 to 3 cm long and 1 to 5 cm wide (Fig. 3). They are smallest in *Callisthene major* and largest in an unidentified species of *Vochysia* (Fig. 3). Within *Vochysia*, those of *V. ferruginea* are the smallest (Fig. 3). Cotyledons are mostly 1.3 to 2.0 times wider than long in *Vochysia*, *Salvertia*, and *Callisthene*, but only 0.8 to 1.3 times wider than long in *Qualea*, and broadest above the middle in *Vochysia* and *Salvertia*. They are broadest around the middle in *Callisthene* and *Qualea* (Table 1; Fig. 3). They are asymmetric or symmetric in *Vochysia* (Fig. 1J and 2A, E–F), as in the embryos, but this may be variable within some species or collections (Table 1). The apex of *Q. grandiflora* was short-acuminate, that of *C. major* ± obcordate, and those of *Vochysia truncate*, rounded, retuse or rarely obcordate (Fig. 1J and 2A, E–F; Table 1). Venation can only be assessed in *Vochysia*, but the pattern is unusual. The midvein forks toward the apex, whether the apex is rounded or lobed, and two strong lateral primaries diverge from the base: in most species, the lateral primaries join with the recurved branches of the midvein to form triangular to obovate intercostal areas (Fig. 1J and 2A, E–F; Table 1). Smaller veins form one or more concentric series of loops around the central intercostal areas.

The cotyledonary stipules in the three species of *Vochysia* described in this study are unusual two-parted structures (Fig. 1K–M; Fig. 2C–D, G). The lower part usually consists of one to three narrow projections between the petioles, usually perpendicular to the hypocotyl, situated at the base of the upper (adaxial) surface of the petiole where the upper ridge or wing of the petiole terminates. The upper part consists of a flattened interpetiolar scale-like outgrowth just above the petioles, initially folded over the terminal bud but becoming erect and visible as the epicotyl expands, completely or partially divided or torn into two to five parts but rarely unlobed. The apex of the lower and/or upper parts often appears gland-like. Neither part appears to be fused over the petioles, and the axillary buds are often visible above the cotyledonary petiole. Although there was some intraspecific variation, the stipules of *V. ferruginea* usually had one lower projection and a lobed upper part and those of *V. guatemalensis* two lower projections and two separate upper parts. The reduced stipules of *V. guatemalensis* have also been described as 2–3 trichomes of a glandular nature (Flores, 1993a), but the thick 3-lobed pair of structures illustrated (fig. 7e) appear rather large and fleshy for trichomes and may be a different form of the variable structures described in this study. Two-parted cotyledonary stipules similar to those of *Vochysia* have not been seen in seedlings of more than 600 dicotyledonous species in 88 families surveyed from Panamá (Garwood, in prep.), although the fleshy cotyledonary stipules of *Lafoensia* (Lythraceae) are similar to the lower stipular parts of *Vochysia*.

Leaves are opposite at the early nodes in *Vochysia*, *Qualea*, and *Callisthene* (Table 2). In *Vochysia*, the pair of leaves at the first node is decussate with respect to the cotyledons and leaves at the second node (Table 2). In *Q. grandiflora*, the first pair of fully developed leaves is parallel to the cotyledons but decussate to the second pair of leaves (Table 2); a pair of 'prophylls' between the cotyledon and first pair of leaves (Thomazini et al., 1973) might be vestiges of the 'missing' pair of decussate leaves or homologous to the interpetiolar cotyledonary stipules of *Vochysia*. Leaves remain opposite into the adult stage in *V. ferruginea*, but become 3- then 4-whorled in *V. guatemalensis* sometime in the sapling stage. The initial axis of *C. major* appears to be plagiotropic, with opposite distichous leaves smaller than the cotyledons, but this will need confirmation because it is difficult to interpret details in the published photograph of the seedlings (Labouriau et al., 1964: fig. 26).

Stem characters are known only from *Vochysia*. The collet, the

**Table 1** Cotyledon characters in seedlings and embryos of Vochysiaceae.

Genus Species	Source	Emer- gence	Posi- tion	Devel- opment	Persistence		Width:Length Ratio	Shape	Base	Apex	Symmetry	Venation	Stipules
					node	months							
<i>Vochysia</i>													
<i>V. densiflora</i> Spruce	18*	–	–	F	–	–	1.7	2	5–7	8	A	–	–
<i>V. duquei</i> Pilg.	15	P	E	Fr	2	>1	1.6–1.9	2–3,6	4–6	3–5	S	1,2	+
<i>V. ferruginea</i> Mart.	6	P	E	F	3–8	>9	1.3–1.9	2	3–6	6–7	A	1–3	f+f,g
	10	–	E	–	–	–	–	–	–	–	–	–	–
	4b	P	E	F	2	–	1.6	2	6	5	S,A	1	f
<i>V. guatemalensis</i> Donn. Sm.	6	P	E	F	3	–	1.2–1.8	2	3–6	3–5	A	1–3	s+s,g
	10	–	E	–	–	–	–	–	–	–	–	–	–
	4a	P	E	F	1	–	1.2–1.3	2	6	4	A	1,4	s,g
	1,5	P	E	F	6	–	1.5	2	4–5	4	A	1,2	–
<i>V. obscura</i> Warm.	18*	–	–	F	–	–	1.4	2	7	4–5	S	–	–
<i>V. surinamensis</i> Stafleu	14	P	E	F?	6	–	2.7	1	–	3–4	–	–	–
<i>V. thyrsoides</i> Pohl	13	–	E	–	–	≈ 12	–	–	–	–	–	–	–
	16	P	E	Fr	1	>12	–	–	–	–	–	–	–
<i>V. tucanorum</i> Mart.	18*	–	–	F	–	–	1.6	2	6–7	3–4	A	–	–
<i>V. sp.</i> (Brazil)	2	P	E	F	–	–	–	1	–	–	–	–	–
<i>V. sp.</i> (Fr. Guiana)	11	P	E	F	–	–	2.1	2	4	5	S	2,5	–
<i>V. sp.</i> (Panamá)	6	P	E	F	1	–	1.4–2.1	2	3–5	4–6	S,A	1–3	s+f,g
<i>Salvertia</i>													
<i>S. convallaridorea</i> A. St.–Hil.	18*	–	–	F	–	–	1.6	2	2–3	4–5	S	–	–
<i>Qualea</i>													
<i>Q. grandiflora</i> Mart.	12	P	E	F	2	>6	–	–	–	–	–	–	–
	3	P	E	F	–	4	–	–	–	–	–	–	–
	17	P	E	F	2	>6	1.1	5	3–4	1	A?	–	P
<i>Q. multiflora</i> Mart.	18*	–	–	F	–	–	0.8–1.3	4	3	9	A	–	–
<i>Callisthene</i>													
<i>C. major</i> Mart.	8	P	E	F?	1–3?	–	1.2–1.5	3	–	5–6	–	–	–
	18*	–	–	F	–	–	1.2–1.6	–	–	–	–	–	–
<i>Erisma</i>													
<i>E. spp.</i>	7*	–	–	R	–	–	–	–	–	–	–	–	–
<i>Erismadelphus</i>													
<i>E. exsul</i> Mildbr.	9	C	H	R	–	–	–	–	–	–	–	–	–
<i>E. sp.</i>	9	C	H	R	–	–	–	–	–	–	–	–	–

Source: 1, del Amo 1979; 2, Duarte 1979; 3, Felipe & Dale 1990; 4a,b, Flores 1993a, b; 5, Gaos 1978; 6, Garwood, this study; 7, Kawasaki, in press; 8, Labouriau et al. 1964; 9, Miquel 1987; 10, Moreira & Arnáez 1994; 11, Oldeman & Fundter, 1986; 12, Paulilo et al. 1993; 13, Paviani & Haridasan 1988; 14, Polak 1992; 15, Ricardi et al. 1987; 16, Rizzini 1965; 17, Thomazini et al. 1973; 18, Warming 1875. \*, all characters based only on the embryonic cotyledon in the mature seed.

Emergence: P, phanerocotylar; C, cryptocotylar.

Position: E, epigeal; H, hypogeal.

Development: F, foliaceous; R, fleshy, presumably with stored reserves; r, somewhat fleshy or succulent, with reserves or stored water.

Persistence: measured as i) the last recorded leaf node to produce leaves while the cotyledons are still present (e.g. node=3, cotyledons still present when leaves produced at node 3) or ii) the length of time [months] that cotyledons persist after germination. These measures underestimate persistence when only the youngest seedling stages have been studied.

Width:Length Ratio: width divided by length.

Shape: 1, obtriangular to shallowly obtriangular, including 'triangular'; 2, depressed obovate; 3, transversely oblong; 4, very widely obovate; 5, transversely widely elliptic to transversely widely oblong; 6 transversely reniform, rectangular-reniform.

Base & apex: 1, short-acuminate; 2, acute; 3, rounded; 4, truncate; 5, retuse to emarginate; 6, cordate, obcordate, 2-lobed; 7, 2-cleft or -parted; 8, 3-lobed; 9, irregular. When blade is asymmetric, the base and/or apex may be unequal on the two sides (e.g. half-cordate, half-rounded) or oblique (e.g. obliquely truncate).

Symmetry of blade: A, asymmetrical; S, symmetrical.

Venation: 1, branches of forked central primary vein join lateral primaries forming a pair of obovate to triangular intercostal areas; 2, palmate or 3-nerved; 3, basal acrobrochidodromous; 4, basal actinodromous; 5, branches of central primary vein forked; lateral primaries each form a closed loop apically, terminating near but not joined directly to the tips of the central vein.

Stipules: s, usually separate; f, usually fused and interpetiolar; f+f, f+s, and s+s, two structures (fused or separate) present at cotyledonary node (first is lower structure, second is upper structure); g, gland-like; +, present; P, 'prophylls' present above cotyledons.

–, Information not available.

Characters in italics were inferred or estimated from illustrations in the citations, not from the text of the original author. Where authors identified the cotyledons as foliaceous, it was assumed that they were also phanero-epigeal.

junction of the radicle and hypocotyl, is annulate in at least three species (Table 2; Fig. 1F). The hypocotyl, epicotyl, and later internodes are usually square, with ridges or wings on each corner (Table 2). Ridges on the hypocotyl continue without interruption into the ridges on the lower margins of the cotyledonary petioles in *V. ferruginea* and *V. guatemalensis* (Figs 1K, 2G; Flores, 1993a, b). In contrast, the wings or ridges on the epicotyl and later internodes

terminate in small narrowly triangular to linear stipules at the top of each internode (Fig. 1O, S; Table 2), with the inner margin and base of the stipules apparently extending above the petiole but not attached to it. The winged stems do not originate directly from decurrent leaf bases, as sometimes suggested, because the attenuate base of the blade narrows into a medial pair of short thin ridges on the upper (adaxial) surface of the petiole, interrupting the lamina

**Table 2** Root, stem, and leaf characters in seedlings of Vochysiaceae.

Genus Species	Source	Collet	Hypocotyl	Epicotyl	Internodes	Phyllotaxis		Leaf stipules
						Nodes 1–2	Later nodes	
<i>Vochysia</i>								
<i>V. duquei</i>	15	a	s	s	–	o	–,v	+
<i>V. ferruginea</i>	6	a	s,w	s,w	s,w	o,d	o,d	+,s
	4b	c	s	–	–	o,d	o,d	–
<i>V. guatemalensis</i>	6	a	s,w	s,w	s,w	o,d	o,w	+,s
	4a	c	s,w	s,w	–	o,d	o,w	–
	1,5	c	c,w	s,w	s,w	o,d	o	+,i
<i>V. surinamensis</i>	14	–	–	–	s,w	o	o,v	–
<i>V. thyrsoidea</i>	13	c	t	–	–	–	–	–
<i>V. sp. (Panamá)</i>	6	–	s,w	w	–	o	–	–
<i>Qualea</i>								
<i>Q. grandiflora</i>	17	–	–	–	–	o,p	–	–
<i>Callisthene</i>								
<i>C. major</i>	8	–	–	–	–	o	a?	–

Sources and authorities for names: see Table 1.

Collet (junction of hypocotyl and primary root): a, annulate ridge present; c, constriction, abrupt change, or other feature present, but nature of structure not discernable from illustration.

Hypocotyl, Epicotyl, and Internode: cross-sectional shape of hypocotyl, epicotyl, and early internodes (about first ten), respectively: s, square to rectangular; c, circular; t, tuberos and circular, at least when older; w, 4 wings or ridges present.

Phyllotaxis:

Nodes 1–2: o, leaves at first node opposite; d, pair of leaves at first node decussate to both cotyledons and pair of leaves at second node; p, pair of leaves at first node parallel to cotyledons and decussate to pair of leaves at second node.

Later nodes: o, leaves opposite and decussate (at least to node 5, sometimes reported up to node 20); d, leaves opposite and decussate on larger seedlings, saplings, and adults; w, leaves whorled on larger seedlings or saplings (and adults), with three or four leaves per node, size of juveniles at time of transition from opposite to whorled leaves unknown; v, juvenile leaves unknown, but adult leaves whorled; a, axis becoming plagiotropic with pairs of leaves distichous.

Leaf stipules: +, small, narrowly triangular to linear stipules present from the first node; i, stipules intrapetiolar; s, stipules separate.

–, Information not available.

Characters in italics were inferred or estimated from illustrations in the citations, not from the text of the original author.

between the blade and wings. It is unclear, however, whether the petiolar ridges are joined to the lateral extensions of the stipules.

Striking ontogenetic changes are seen in hair morphology in *Vochysia ferruginea* (this study). The epicotyl and first leaves are only sparsely pubescent below, but stems and leaves at higher nodes become progressively more densely pubescent. Hairs on early internodes and lower leaf surfaces are nearly sessile, appressed, and T-shaped, with straight arms of equal length; those on later leaves and stems are short-stalked, ascending to erect, 2-branched, with the longer arm curved to coiled and about eight times longer than the shorter arm. Hairs on the adult leaves are similar, except the branches are even more unequal in length (Garwood, pers. obs.). On seedlings to adults of *V. ferruginea*, hairs on the midrib above are always simple. In *Vochysia* sp. (Garwood 135 and Hampshire & Whitefoord 269), hairs on the epicotyl and eophylls were similar to those on *V. ferruginea*. In contrast, hairs on the young expanding leaves of *V. guatemalensis* were simple and basifixed, but these were usually sparse or absent on mature leaves (Flores, 1993a; this study). All parts of *V. duquei* are glabrous (Ricardi et al., 1987).

Seedlings from the Brazilian cerrado have a number of special morphological adaptations to the dry cerrado environment (Labouriau et al., 1964; Rizzini, 1965; Paviani & Haridasan, 1988). *Vochysia thyrsoidea* has ± fleshy succulent cotyledons, a thick watery hypocotyl which is mostly buried, minute eophylls which remain hidden between the cotyledons, greater growth of the taproot rather than shoot in the first few months, and a swollen subterranean organ which forms from the hypocotyl and upper part of the taproot in the first two years. *Qualea grandiflora* also forms a swollen underground organ.

## Phylogeny

There have been no phylogenetic analyses of relationships within Vochysiaceae. Since the completion of Stafleu's (1948–1954) monograph more than 40 years ago, the numbers of collections and species described have increased, but major systematic work has been limited to elevating one section of *Qualea* to *Ruizterania* (Marcano-Berti, 1969) and monographing *Erisma* (Kawasaki, in press). Fruit and seed characters have long been important in delimiting genera within the family, but the utility of seedling characters has been untested because seedlings have not been available for study. The potential of the new seedling and seed characters described above to contribute to phylogenetic and systematic studies is discussed here. If such traits look promising, data on more species should be collected.

Phanero-epigeal seedlings are reported only from Vochysieae, and crypto-hypogaeal seedlings from Erismeae, following the current tribal division. In Vochysieae, shape characters of the foliaceous cotyledon fell into three groups corresponding to *Qualea*, *Callisthene*, and *Vochysia/Salvertia*, although some variation occurred in all groups. Symmetry of the cotyledons varied most in *Vochysia*, and veneration and ptyxis of the embryonic cotyledons in *Qualea*. Several traits generally uncommon in dicotyledon seedlings occur together in *Vochysia*, including unusual cotyledonary stipules and cotyledonary venation, annulate collet, and winged hypocotyls and early internodes, but these have not been assessed in many species or other genera. Supra-cotyledonary prophylls, also unusual in dicotyledon seedlings, were reported in one species of *Qualea*. The existence of considerable variation in cotyledon characters, and the presence of many unusual seedling characters in this small sample of

about 20 species (Tables 1–2), suggests further study of other taxa would be profitable.

Ontogenetic changes from the seedling to adult stages can also be important phylogenetic characters. In *Vochysia*, leaves of adults are either opposite or 3- or 4-verticillate, but the first seedling leaves of all species described are opposite (Table 2). In *V. guatemalensis*, leaves remain opposite at early seedling nodes, but gradually become 3- then 4-verticillate in larger saplings (Flores, 1993a). Although presence of opposite seedling leaves in all taxa would not be phylogenetically informative, the timing of the switch from opposite to verticillate leaves may provide a useful character. Adult leaves are also verticillate in *Salvertia* and some species of *Erismia*, but opposite in other taxa (Stafleu, 1948–1954).

Pronounced ontogenetic changes in hair morphology were observed in *Vochysia ferruginea*, but not in *V. guatemalensis*. Because studies of ontogenetic changes of trichomes on leaves of seedlings and adults have helped identify groups of species within the large and complex genera of *Solanum* and *Rhododendron* (Seithe 1979, 1980; Seithe & Anderson, 1982), further study would be warranted. Unfortunately, the morphology of hairs in *Vochysia* is poorly known. They have been described as simple or sometimes unicellular and 2-branched (Warming, 1875; Metcalfe & Chalk, 1950); hairs have arms of equal length and short stalks in at least one species (Shanmukha Rao & Vijayalakshmi Sarma, 1992). Stafleu (1952) indicated that simple and biramosse hairs occurred in Vochysiaceae, but did not specifically describe those of *Vochysia* (Stafleu, 1948), although frequent references to ‘peculiar indumentum’ or ‘characteristic indumentum’ suggests that their morphology is unusual.

An examination of adult specimens of *Vochysia* at BM indicates that species with 2-branched or simple hairs are both common (Table 3). The distribution of simple and branched hairs is clearly not random with respect to the sections of *Vochysia* delimited by Stafleu (1948). Branched hairs are especially abundant in subsection Ferrugineae, which contains *V. ferruginea*. There was considerable variation among species in the morphology of the branched hairs of the adult stage, ranging from nearly sessile appressed T-shaped hairs with straight branches of equal length, to long-stalked erect 2-branched hairs with curled arms of equal or unequal length (Garwood, pers. obs.). In some species, the smaller arm was so reduced in length that the hair could easily be misinterpreted as simple, suggesting that at least some of the simple hairs in *Vochysia* might be derived from much-reduced branched hairs, as occurs in Malpighiaceae (Anderson, 1990). The range of hair morphology from the seedling to adult stages in *V. ferruginea* spans nearly the entire range of branched hairs seen in the genus. Therefore, examining the ontogeny of branched hairs might reveal similarities in the early stages that would be phylogenetically informative in comparison with other species of *Vochysia*, or other genera. Hairs are also simple or 2-branched in *Qualea* (Stafleu, 1953), but stellate in *Erismia* (Warming, 1875; Stafleu, 1954), and simple in *Callisthene* (Stafleu, 1952), *Salvertia* (Garwood, pers. obs.), and *Erismadelphus* (Garwood, pers. obs.).

Seed, fruit, and seedling characters also bear on the higher order relationships of the family. Vochysiaceae has usually been included in the Polygalales with Polygalaceae, Trigoniaceae, Malpighiaceae, Xanthophyllaceae, Tremandaceae, and Krameriaceae (Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981). Boesewinkel & Venturilli (1987) used anatomy of the seed coat to reassess the position of the family in Polygalales. They concluded that only Polygalaceae and Xanthophyllaceae should be retained in the Polygalales, and that the relationship of Vochysiaceae and the remaining families needed further study. Reviewing numerous floral and vegetative characters in Malpighiaceae, Anderson (1990) decided that Malpighiaceae was most similar to Vochysiaceae and Trigoniaceae and least similar to Polygalaceae and Krameriaceae. The presence of 2-branched unicellular hairs in Vochysiaceae, Trigoniaceae, and Malpighiaceae, and their absence in Polygalaceae, also supports this grouping (Shanmukha Rao & Vijayalakshmi Sarma, 1992).

Recent molecular analyses of the angiosperms using the chloroplast gene *rbcL* also supported the break-up of the Polygalales, but not the grouping of Vochysiaceae with Malpighiaceae and Trigoniaceae (Chase et al., 1993). Instead, Vochysiaceae, represented by *Qualea*, fell within the Myrtales. A more detailed study of Myrtales using the same gene confirmed the Myrtalean affinities of Vochysiaceae, represented by *Vochysia*, *Erismia*, and *Qualea* (Conti et al., 1996). Vochysiaceae was sister group to the Myrtaceae and these, with Heteropyxidaceae and Psiloxylaceae, formed the sister clade to that containing Melastomataceae, Memecylaceae, and other families. Work with chloroplast gene *matK* also supports placement of Vochysiaceae in Myrtales, but it falls between Myrtaceae (with Heteropyxidaceae and Psiloxylaceae) and Melastomataceae (with Memecylaceae) (P. Wilson, pers. comm.).

Previous systematic treatments based on morphology have never included Vochysiaceae in the Myrtales (Conti et al., 1996), regard-

**Table 3** Distribution of simple and branched hairs in *Vochysia*.

Section	Subsection	Number of species				
		Described by Stafleu (1948)	Examined for study	Type of hair		
Simple	Branched			Unknown		
Vochysiella	Decorticanthes	10	6	6	0	0
	Calophylloideae	10	7	6	0	1
Ciliantha	Micranthae	11	9	8	0	1
	Lutescentes	23	13	6	4	3
	Discolores	3	2	0	2	0
	Chrysophyllae	1	1	1	0	0
	Megalanthae	5	3	3	0	0
	Ferrugineae	31	22	1	18	3
Pachyantha	–	3	0	–	–	–

Type of hair: simple, only simple unbranched hairs present on leaves, stems, and reproductive parts; branched, some or all of hairs present branched, including T-shaped hairs; unknown, specimens glabrous or hairs too small or dense to characterize. Leaves, stems, and inflorescences of one to several specimens of each species at BM monographed by Stafleu (1948) were examined under a 40x dissecting microscope.

ing this relationship as so remote that the presence of two of the most definitive Myrtales characters, vestured pits in the secondary xylem and bicollateral vascular bundles in the primary stem, was not considered significant (van Vliet & Baas, 1984). In retrospect, many vegetative characters of Vochysiaceae are equally at home in Myrtales (*sensu* Dahlgren & Thorne, 1984) as in Polygalales, including opposite or verticillate leaves with entire margins, brochidodromous venation, and stipules. The highly zygomorphic flowers with one fertile stamen are, however, unusual in the order (Conti et al., 1996). When a thorough morphological analysis of the relationship of Vochysiaceae within Myrtales is undertaken, several seedling and seed characters described for Vochysiaceae deserve further study.

Vochysiaceae share other vegetative characters with Myrtales, including the occasional presence of 2-branched unicellular or tufted hairs in Combretaceae, Lythraceae, and Myrtaceae (Metcalf & Chalk, 1950). Cotyledonary stipules, generally uncommon in dicotyledons, occur as rudimentary glandular structures in some Lythraceae, Onagraceae, and Myrtaceae, and as 2- to 3-lobed structures or glandular processes near the basal margins of the blade in other groups of Myrtaceae (Weberling, 1984). The latter type might be homologous to the unusual cotyledonary stipules of *Vochysia* (Flores, 1993a; this study), which are composed of an upper lobed part and lower possibly glandular part.

Wings are well-developed on adult stems in some Lythraceae and Penaeaceae, and often develop auricles at the apex, which are distinct from the rudimentary stipules found closer to the petioles (Weberling, 1984). In Lythraceae, auricled wings are already present at the seedling stage in *Lafoesia* (Garwood, in prep.). Wings are well-developed on seedlings of *Vochysia*, although usually reduced to ribs on adults (Stafleu, 1948; Garwood, pers. obs.). As the small stipules of *Vochysia* occur at the apex of the wings, they may be homologous to the auricles at the apex of the wings of these Myrtales, rather than the small, often dissected, stipules characteristic of Myrtales (Weberling, 1984). If so, *Vochysia* may lack true stipules. Herbarium specimens of *V. ferruginea* and *V. guatemalensis* seedlings were carefully examined for the presence of dissected or rudimentary stipules over the petioles, but none were seen (Garwood, pers. obs.). The occasional presence of a minute shrivelled structure, however, suggests that actively growing seedlings should be examined to verify whether minute caducous stipules are present but hidden by the small erect expanding leaves. In seedlings of Myrtaceae, auricles are lacking on the winged epicotyl and later internodes of *Psidium* and *Calycolpus* and on the winged hypocotyl of *Myrcia*, and wings are lacking in *Eugenia*, but all have rudimentary gland-like stipules (Garwood, in prep.).

Seeds of Vochysiaceae and Myrtales generally lack endosperm and arils and have straight or slightly curved embryos (Cronquist, 1981; Dahlgren & Thorne, 1984). A fibrous exotegmen and an endotestal crystal layer are found in *Qualea* and some Lythraceae, Combretaceae, and Onagraceae, but the exotegmen lacks fibres and is crushed in *Vochysia* and some Melastomataceae and Myrtaceae (Corner, 1976; Dahlgren & Thorne, 1984; Boesewinkel & Venturelli, 1987). The embryonic cotyledons are variously folded in Vochysiaceae and many Myrtales, with folding frequently described as 'spiral' in *Vochysia* as well as Combretaceae and Oliniaceae (Dahlgren & Thorne, 1984). As brief descriptions of vernation and ptyxis in Vochysiaceae are generally incomplete or incorrect (see above), further detailed studies should be carried out throughout the order.

## Ecology

Seed germination has been the most frequently studied aspect of the seed and seedling ecology of Vochysiaceae. Germination is usually rapid, occurring 1 week to 3 months after seed dispersal or sowing in species of *Vochysia*, *Salvertia*, and *Qualea* from both cerrado and rainforest (Rizzini, 1965; Thomazini et al., 1973; Macedo, 1977; Duarte, 1979; Sabatier, 1985; Paviani & Haridasan, 1988; de Godoy & Felipe, 1992a; Moreira & Arnáez, 1994; Flores 1993a, b; this study; M. Bustamante, pers. comm.; P.E. Oliveira, pers. comm.; P. Wilson, pers. comm.). Chemical or mechanical scarification of the seed coat, or its complete removal, may hasten germination in *Q. grandiflora* (Felippe, 1990; Felippe & Dale, 1990), but is not required (M. Bustamante, pers. comm.; P.E. Oliveira, pers. comm.; P. Wilson, pers. comm.). Germination is not inhibited by dark or shaded conditions in *Q. retusa* Spruce ex Warm., *Q. grandiflora*, or *V. ferruginea* (Macedo, 1977; Felippe, 1990; this study), although it can be somewhat depressed in direct sunlight (Flores, 1993b). Recently dispersed seeds of *V. maxima* Ducke buried under the leaf litter either lost viability or had germinated within 2 months (Viana, 1990). Thus, there is no indication of any type of seed dormancy in the family, and seeds should form transient, rather than persistent, seed banks under natural conditions.

Under artificial conditions, seeds of *Qualea cordata* Spreng., *Vochysia guatemalensis*, and *V. ferruginea* retained high viability for at least 2–3 months when stored at room temperature and humidity (de Godoy & Felipe, 1992a; Flores, 1993a, b), in spite of a relatively high initial moisture content in *Vochysia* (23–32%, fresh weight basis). Reducing the moisture content extended viability of the apparently orthodox seeds, although they were intolerant of chilling (Flores, 1993a). The potential to store seed should promote the ongoing silvicultural development of the family.

Seeds of all species are wind-dispersed, as indicated by the morphology of seeds of Vochysiaceae and indehiscent fruits of Erismaceae, except *Erisma calcaratum* (Link) Warm. from the Amazonian varzea, which is water-dispersed (Stafleu, 1954). In tropical forests, seeds of *Vochysia maxima* are dispersed near the parent, mostly  $\leq 30$  m from the trunk (Viana, 1990), seedlings of *V. maxima* and *V. ferruginea* persist in the shaded understorey (Viana, 1990; Garwood, pers. obs.), but growth is fast only in treefall gaps and larger openings (Viana, 1990; Boucher et al., 1994). In plantations, seedlings of *V. guatemalensis* and *V. ferruginea* can reach 2–3 m tall within three years (Flores 1993a, b). Thus, tall canopy *Vochysia* appear to be gap opportunists, regenerating from a persistent seedling bank following disturbances throughout the year. Regeneration of *Qualea* may follow a different pattern. Following a severe hurricane, most of the severely defoliated adults of *Q. paraensis* Ducke survived but there was no regeneration from seedlings or saplings; in contrast, all the equally abundant and severely defoliated adults of *V. ferruginea* died, but there was extensive regeneration from seedlings and saplings (Boucher et al., 1994). If this pattern is typical, species of *Vochysia* may be more amenable to sustainable management or plantation development than *Qualea*.

In the drier and more open cerrado, seedlings of *Qualea grandiflora*, *Q. cordata*, and *Vochysia thyrsoidea* appear to grow inherently slowly, with neither extra moisture nor nutrients promoting rapid growth (Rizzini, 1965; de Godoy & Felipe, 1992b; Paulilo et al., 1993; Felippe & Dale, 1990). Although the basis for the slow growth is not understood, many species develop special morphological adaptations to the cerrado environment, such as large subterranean storage organs and thick succulent cotyledons (Labouriau et al., 1964; Rizzini, 1965; Paviani & Haridasan, 1988).

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